

Symposium

Ecological Resistance in Theory and Practice¹

CARLA M. D'ANTONIO and MEREDITH THOMSEN²

Abstract: Ecological resistance refers to the biotic and abiotic factors in a recipient ecosystem that limit the population growth of an invading species. Although there is interest in applying this concept to the management and restoration of habitats influenced by damaging, invasive species, practical difficulties in restoring resistance have inhibited its broad-scale incorporation. Also, some ecologists have argued that resistance is unimportant in generating landscape pattern casting doubt on its potential usefulness in large-scale management. In this study, we argue that despite temporal and spatial fluctuations in resistance being the norm, the concept provides a valuable foundation for a more sustainable approach to long-term weed management. This goal should be achievable through identification and manipulation of successional processes in natural communities.

Additional index words: Biotic resistance, community invasibility, ecological restoration, weed control.

INTRODUCTION

Charles Elton, in his 1958 book *The Ecology of Invasions by Animals and Plants*, introduced the term ecological resistance. He defined it quite broadly as those “forces of nature,” natural processes or ecosystem properties that contribute to a reduction in the rate of establishment and spread of introduced species. Thus, although the origin of the concept is typically ascribed to Elton, it is clear from this definition that it derives from basic questions about controls on community composition that have always been fundamental to ecology. What Elton (1958) contributed was to apply these general principles specifically to the question of what limits the spread of introduced species. Even more recently, the concept has been applied to community restoration or enhancement projects undertaken to reduce the likelihood of invasion (or reinvasion) by unwanted species.

Ecological resistance includes both biotic and abiotic resistance factors. Biotic resistance includes competition, predation or herbivory, pathogens, and the absence of mutualist species necessary for the invader to establish and spread (D'Antonio et al. 2001; Richardson et al. 2000). Abiotic resistance includes such factors as minimum annual temperature, soil characteristics, and drought or disturbance conditions that make it difficult

for some invading species to thrive (Baker 1986). Here we will outline several elements of resistance that likely occur in managed ecosystems and provide examples of research on or management strategies that could make use of this resistance. Throughout, we address whether or not the sources of ecological resistance in plant communities can be understood and then controlled or used to aid in the management of invasive, undesirable species.

SOURCES AND APPLICATIONS OF RESISTANCE

Most studies that have experimentally evaluated factors limiting the success of particular invaders have focused on resistance from competition by residents. For example, the large body of research on the role of species richness and functional group diversity in invasion resistance is based on the premise that when more species or functional groups are present, that area is more likely to be resistant because residents are making complete use of available resources (Levine and D'Antonio 1999) or because higher diversity assemblages are more likely to contain species with larger body size or higher productivity which then play a disproportionate role (i.e., the sampling effect: Huston 1997; Wardle 2001). Numerous studies at the local (pot or plot) scale have found that arriving seeds of invaders are less successful in higher diversity plots and that this diversity correlates with lower resource availability (Kennedy et al. 2002; Levine 2000, 2001; Naeem et al. 2000; Tilman 1997),

¹ Received for publication July 19, 2004, and in revised form July 23, 2004.

² Lead Scientist, U.S. Department of Agriculture–Agricultural Research Service, 920 Valley Road, Reno, NV 89511; Ph.D. Candidate, Department of Integrative Biology, University of California, Berkeley, CA 94720-3140. Corresponding author's E-mail: dantonio@socrates.berkeley.edu.

although this result is not universal (e.g., Robinson et al. 1995; Wiser et al. 1998). The positive results are encouraging to restoration practitioners because they suggest that if restoration succeeds in establishing high cover of competitive residents (e.g., ones that have high rates of acquisition and storage or monopolization of resources), the probability of future establishment of invaders can be reduced (but see discussion of Stohlgren et al. 1998, 1999, 2003 below). Nonetheless, there are very few examples of large-scale restoration projects that have focused on restoring competitive resistance or have measured success in reducing invasion by doing so.

The recommendation to restore competitive residents is complicated by the fact that competitive resistance often interacts strongly with abiotic resistance factors including climate and fluctuations in soil resource availability. For example, Davis et al. (2000) have argued that invasion resistance is a function of resource uptake by the vegetation vs. resource supply rates. When uptake by the plant community is reduced because of climatic fluctuations, disease or disturbance, resistance decreases because unused resources exist. Similarly, a lag between enhanced resource supply rates (perhaps driven by weather) and resident uptake can result in periods when excess resource availability makes a site more susceptible to invasion. They demonstrate experimentally that even short resource pulses can translate into increased invasion in some systems (Davis and Pelsor 2001). Rather than viewing the competitive environment as static, this simple framework provides a dynamic view in which communities have windows of greater and lesser susceptibility to invasion. In a management context, this means that at certain times and places, increases in resource supply will create conditions favorable to invasion even if residents are well established. Because disturbance often causes increased resource supply and because some disturbance occurs in virtually all communities (Sousa 1984), this framework suggests that all communities are likely to have at least some windows of vulnerability to invasion. Depending on the scale of disturbance events (or known resource pulses), the post-disturbance window can be targeted for management actions including early detection and rapid response to incipient invader populations.

Disturbance can also directly prevent the establishment of certain species, independent of competitive effects, and can therefore itself be a form of resistance. Invaders that are not adapted to fire, for example, should be unable to invade in ecosystems with high fire frequencies. Thus, an understanding of the effect of historic

types of disturbances on species composition, and of the disturbance responses of desired vs. unwanted species, is essential to using disturbance as a management tool (e.g., Kotanen 1997). Furthermore, the complexities of both natural and managed disturbance effects cannot be overstated. For example, Platt and coworkers (Drewa et al. 2002; Platt 1999; Platt and Gottschalk 2001; Platt et al. 2002) have demonstrated that the timing and intensity of fires can have a dramatic effect on species composition in highly diverse pine savanna ecosystems in the southeastern United States. Historically, fires occur in the wet or growing season, tending to select against many invaders or less desired species (Drewa et al. 2002). By contrast, human management involving use of prescribed fire has changed fire timing to the dry or dormant season, which has tended to promote less desirable plant communities. But there are some species of invaders such as cogongrass (*Imperata cylindrica*) that invade even when pine savannas are managed with historic fire regimens, thereby constraining use of “natural disturbance” to keep invaders out (W. J. Platt, personal communication).

Another source of biotic resistance that has received some recent attention is the negative effect that herbivores and seed predators can have on unwanted plant species (Maron and Vila 2001). The introduction of insect biocontrol agents is typically based on the assumption that such resistance is absent and will be important in reducing further spread if appropriate herbivores can become established. Recently, several investigators have found that native vertebrate herbivores can limit the establishment of invaders (Bossard and Rejmanek 1994; D’Antonio 1993; D’Antonio et al. 1993; Mack 1996; Maron and Vila 2001). However, it is not clear that the process is general enough to be used in management or that management-level manipulations of native vertebrate herbivores are practical. However, managers may want to ascertain that native grazers and browsers do not contribute importantly to biotic resistance before taking actions that could decrease their population sizes or effectiveness. In contrast, livestock grazing has been used effectively to control establishment and population size of particular undesirable invaders such as yellow starthistle (*Centaurea solstitialis*) in California (e.g., Kephart 2001; Thomsen et al. 1993) or other pasture weeds (e.g., Popay and Field 1996). However, the long-term sustainability of controlling invaders in rangelands or wildlands with livestock grazing is controversial.

An understanding of the importance of different types of resistance can sometimes be used to strengthen man-

agement through dual or integrated management actions. For example, plant competition and herbivory can be used synergistically to limit invasion. McEvoy et al. (1993) found that the success of biological control agents in controlling tansy ragwort (*Senecio jacobaea*), a pasture weed in Oregon, was strongly affected by the competitive environment provided by the background vegetation: control was more effective, where the background vegetation provided strong competition. The combination of herbivores and competition could control invader success even in the presence of soil disturbance that stimulated localized seed germination of the invader. Similarly, Notzold et al. (1997) found that biocontrol agents had a greater negative effect on purple loosestrife (*Lythrum salicaria*) when plant competition was also more intense. Wilson and Partel (2003) found that combining either mechanical or chemical control of crested wheatgrass (*Agropyron cristatum*) with increased resource competition from native species was the most effective means of achieving long-term control of this perennial grass invader in a Canadian prairie restoration.

In addition to trying to restore or enhance competitive resistance, management strategies can try to control changes that might be occurring in abiotic resistance. For example, until recently, California serpentine grasslands were less invaded by Eurasian annual grasses than the surrounding sandstone-derived soils (Harrison 1999; McNaughton 1968; Mooney et al. 1986). Those native species that can tolerate or are adapted to serpentine soils have thrived in these weed-free sites. Huenneke et al. (1990) demonstrated that addition of N alone could overcome the abiotic resistance of the serpentine soils and result in increased invasions by Eurasian annual grasses. Since then, atmospheric N deposition has become widespread in the southern portion of the San Francisco Bay region (Weiss 1999), with high levels of ammonium deposition because of catalytic converters in automobiles (Kean et al. 2000). Simultaneous with this increase in ecosystem N availability, serpentine plant communities in the region have been widely invaded by exotic grasses, to the detriment of native species (Weiss 1999). This regional-scale, directional change in N availability is being managed at a local scale by mowing or grazing to remove nitrogen-laden plant biomass and prevent resource monopolization by invasive N-loving grass species (Weiss 1999, 2002).

RESISTANCE IS PROBABILISTIC AND SCALE DEPENDENT

Stohlgren et al. (1998, 1999, 2003) have argued that small-plot experiments reveal very little about the even-

tual patterns of invasion that are detected at the landscape scale calling their importance into question. Their data suggest that resource-rich sites tend to have high diversity of both native and nonnative species and hence their title phrase, "the rich get richer" (Stohlgren et al. 2003). Although the case can clearly be made that the strong effects of competition seen in some small-plot studies can be overwhelmed by landscape-scale phenomena (e.g., Brown and Peet 2003; Levine 2000, 2001; Stohlgren et al. 2003), this should not be interpreted to mean that resistance is inapplicable to pasture and landscape-scale restoration projects.

Instead, as several authors have stressed, resistance is probabilistic and should be expected to vary across space and time; it is not a deterministic factor (Crawley 1989; D'Antonio et al. 2001; Levine and D'Antonio 1999). It may also vary with each combination of invader and invaded-habitat type. Even if factors affecting landscape-scale diversity overwhelm local-scale resistance mechanisms in creating landscape pattern, local resistance can still slow invasion. For example, in many grazed areas, animal effects, biodiversity, strength of competition, and degree of invasion all are higher in the riparian areas and lower on the surrounding slopes (Stohlgren et al. 2003). The fact that competition and invasion are correlated in these systems does not mean that management strategies to increase competition from residents in the stream corridors would not help decrease invasion by particular invaders. Furthermore, even if resistance cannot function to completely repel a given invader from a specific site, as might be evidenced by regional patterns of high abundance of that species in that habitat type, it could still increase the amount of time available for managers to control invader populations, and perhaps ultimately keep the site uninvaded. In terms of classic weed population patterns and the timing of control, resistance can delay the onset of high population growth rates or increase the lag phase often seen in incipient invasions (e.g., Hobbs and Humphries 1994) allowing more time for control.

DIFFICULTIES IN RESTORING TOWARD RESISTANCE

One of the biggest challenges in incorporating the concept of resistance in management is that resistance will always be case specific: a process or characteristic that constitutes resistance to the invasion of one unwanted species in a specific ecosystem can encourage the spread of another weedy species in that or another system. Furthermore, some biotic and abiotic resistance factors are likely to have negative effects on the popu-

lations of desirable plant species as well as those of unwanted ones. For these reasons, ecological resistance will be most helpful in the management of systems in which desirable species differ strongly from unwanted ones in their responses to elements of resistance, perhaps because of differences in phenology, growth form, or small-scale distribution patterns. Resistance may also be most useful and achievable in regions where one or a few natives can readily assume dominance. Finally, resistance may also be an especially useful concept in the management of uninvaded systems; understanding what has kept certain areas free from undesirable species would be an important step toward keeping them that way.

In addition, in many degraded ecosystems, restoring for a more resistant plant community is made all the more challenging by a lack of understanding of the historic context that led to degradation or even a lack of knowledge of the composition of the predegradation plant community (e.g., Hamilton 1997). If forces that counteract resistance and potentially lead to degradation are not well understood and controlled to the extent possible, then efforts to establish resistant communities are not well spent.

Finally, in many situations, native species that could confer resistance to invasion of an undesirable species may not be available. This may be because of a problem of seed availability or of limitations to the regional species pool, including harsh restoration conditions that no local native species can tolerate. In such situations, it may be desirable to use introduced species to accomplish the goal of suppressing a highly undesirable invader. For decades, managers have argued that in the Great Basin, competitive resistance from introduced crested wheatgrass can suppress cheatgrass (*Bromus tectorum*) (Hull and Stewart 1948), a species that is much less desirable in terms of effects on wildlife and fire-promoting properties (Knick and Rotenberry 1995; Knick et al. 2003; Whisenant 1990). Crested wheatgrass may germinate and establish better under a wider range of conditions than most native Great Basin species, a point that argues further in favor of its use (Hull 1974). However, others have argued that crested wheatgrass is also a superior competitor to native species (e.g., Eissenstat and Caldwell 1988), interferes with their establishment (Hull and Klomp 1966; Marlette and Anderson 1986), and is controversial in its wildlife value (Johnson 1986; McAdoo et al. 1989). In this system, the goal of increasing resistance to cheatgrass invasion (by planting crested wheatgrass) appears to stand in opposition to other conservation concerns.

As these examples illustrate, using ecological resistance as a guiding principle will not save managers from having to make difficult decisions involving benefits vs. risks of various management actions. Ultimately, however, it could lead to more sustainable management for desired plant communities.

CONCLUSIONS

Sheley and Krueger-Mangold (2003) presented a management strategy for weed control in rangelands based on successional theory, in which they recommend that disturbance, colonization, and species performance be manipulated to create stable, invasion-resistant communities. Their stated goals include developing a universal approach that is less site specific than traditional weed management and one that offers more predictable outcomes. However, as both practical experience and the plant ecology literature inform us, plant community change often differs from the predictable, linear progression postulated by traditional successional theory, and communities can rapidly convert to other assemblages when they cross thresholds (e.g., Beisner et al. 2003; Lauenroth and Coffin 1992; Westoby et al. 1989). As Sheley and Krueger-Mangold (2003) themselves point out, disturbance can reset a successional progression or put it onto a new trajectory altogether. We agree with these authors that their strategy could respond successfully to these types of nonequilibrium dynamics, through the intentional use of disturbance and adaptive management. However, we also believe it is worthwhile to explore the possibility of using a broader concept than succession as the basis for an ecologically based management scheme that involves controlling undesirable species.

In this study, we have stressed the utility of ecological resistance as an alternative organizing principle for ecological weed management. A restoration strategy based on increasing resistance as the goal, using the processes of succession in whatever means are most appropriate for a given system, including management of the propagule supply rate of exotic species ("controlled colonization" in Sheley and Krueger-Mangold 2003), could build upon the framework set forth by Sheley and Krueger-Mangold (2003) and free it from limitations of traditional successional theory. Both schemes would represent a move beyond top-down control of weeds through chemicals, mechanical clearing, or insect herbivores and instead simultaneously use top-down and "bottom-up" methods for managing vegetation in rangeland or wildland settings (e.g., McEvoy and Coombs

1999). To date, very few published examples can be found where such holistic approaches have been taken, but emerging collaborations between weed scientists, managers, and ecologists should ultimately reverse this trend.

ACKNOWLEDGMENTS

We thank the U.S. Department of Agriculture—Agricultural Research Service and National Science Foundation for financial support and conference organizers for making this symposium possible. We also thank Jeanne Chambers and two anonymous reviewers for comments on an earlier draft.

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